Autonomous Evolution in Plants

Differences in plant and animal evolution

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CONTENTS

Page

Summary - - - - - - - - - 103
1. Introduction - - - - - - - - - 104
2. Survival level and *patio ludens* - - - - - - - 107
   Anatomical features and structural fitness of Gymnosperms - - 109
3. Pre-adaptations in plants - - - - - - - 111
4. Early differentiation - - - - - - - - 112
5. Saltatory evolution in plants - - - - - - - 113
6. Gliding evolution in animals - - - - - - - 117
7. Co-evolution of animals and plants - - - - - - 119
   Evolution of orchids - - - - - - - - 121
   Evolution of figs - - - - - - - - 122
8. Reticulate phylogeny - - - - - - - - 123
9. Embryology and ontogeny - - - - - - - 124
References - - - - - - - - - 125

Summary

It is argued that after 'decisions' were made in the early stages about the basic matrix of plant life later evolution followed in an autonomous way, not as a consequence of the competition/selection principle.

Evolution of plants is characterized by their passive tolerance and lack of active aggression. Their main struggle is to evolve against the environment; mutual competition is no agency for their evolution. Animal evolution has, besides this same struggle, a second impetus by competition.

Under this dual pressure animal evolution is proceeding more rapidly and form-making is more abundant, and has led to more complicated specialized structural and behavioural development than in plants because of sexual selection, which is absent in plants.

Competition and survival of plants is more passive and mainly directed against the inanimate environment. This tolerance led to a slower and conservative evolution.

The survival level, which tops all requirements necessary for survival for a certain place and time, lies much lower in plants than in animals and allows for plants a greater free space (*'patio ludens'*) for structural development of non-adaptive characters, which fall beyond competition, selection, and adaptation. This free space in animal development is generally considered to be very narrow.

So-called 'pre-adaptations' in plants have not come into existence because of competition pressure, and is a misleading term in evolutionary sense.

In early differentiation structural decisions for later phyla may well have been made by chance, or these characters may have had in those early stages a lower 'genetical weight' than they got during later establishment.

In plants, the usual way of evolving evolutionary development is through sudden (saltatory) change which is amongst others proved by preponderance of allopolyploid and aneuploid chromosome numbers.

This saltatory evolution proceeded through a small number of specimens.

Saltatory development may also have occurred through sudden change of a few genes which physiologically upset pathways to morphogenesis, partly through neoteny, and gave rise to systematical teratologies, and thus to creation of isolated taxa.

Racial segregation may have led to new species but in plants only in exceptional cases (in long isolation): the term micro-evolution used for this development should be abandoned for plants.

It seems not possible as yet to translate structural changes in genetical terms and define the constancy in genetical weight of genome structure, though there must be a considerable genetical difference between characters common to phyla and those common to families, genera and species. It is peculiar that by a sudden saltation of a 'physiological gene' a very constant structure may be upset, for example by a peloric form in an orchid.

In animals on the other hand 'gliding evolution' by gradual accumulation seems to be the usual way of development. This is attributed to competition and sexual selection, and it goes by populations, through *convivia, commiscua* and *comparia.*

Mutations irrelevant to divergent survival may be possible but they will play a minor role, as *patio ludens* is for animals a very narrow measure. Saltations, if they occur, must be quite exceptional.

Co-evolution of plants and animals is usually a one-sided affair, in which changes in plant structure occur first, and adaptation by animals follows. Except for negligible exceptions plant evolution goes independent of animal evolution in an autonomous way; novelties arising in plants are exploited by animals for their evolution and specialization.

This does not exclude that in a restricted number of cases plants got into a situation where animal action became a vital factor for their survival, as in orchids and figs. In these cases animal populations have forced their way of gliding evolution on that of plants, but even in these cases changes of plant structure do not arise perforce of competition among the plants themselves. their changes remain autonomous, it is the animals which adapt themselves.

It is argued that, whereas in the gliding, divergent evolution of animals there will be hardly any chance of reticulate phylogeny, though their will be of course reticulate affinity.

In plants, however, it has been shown that reticulate phylogeny has played an important role in their evolution.

Finally attention is given to the basic difference between animals and plants in their embryological and ontogenetical development which must have had essential implications for their evolution.

1. Introduction

It is, I believe, generally accepted that evolution in plants and animals is caused by similar impulses and that its mechanism(s) has been the same for both. It should be remarked that this holistic principle is philosophically an extremely attractive axiom. It should, however, also be remarked that the development of evolutionary theory has largely been in the hands of zoologists and zoo-palaeontologists. They had of course no reason to check whether the axiom is fully valid for plants or whether there are differences, either in degree or in quality.

From the side of botanists there have been, as far as I can remember, remarkable few queries about the validity of the holistic axiom. And those I know of concern only the proportional speed of evolution.

J. D. Hooker (1859: xii, footnote) pointed to the marked contrast of the showy, vivid differentiation of the fauna as compared with the conservative, rather monotonous development of the plant kingdom, writing: "the much narrower delimitation in area of animals than plants, and greater restriction of Faunas than Floras, should lead us to anticipate that plant types are, geologically speaking, more ancient and permanent than the higher animal types are, and so I believe them to be, and I would extend the doctrine even to plants of highly complex structure". The idea that changes in the development of the Angiosperms have been extremely slow was also stressed by Hamshaw Thomas (1961: 3).

It appears in fact, that certain types of life, especially among the bacteria and algae, have persisted over immense periods, some two, or at least one and a half billion years, before showing further evolutionary development.

It is true that this observation relates only to the quantative aspect, the speed of evolutionary progress, but it leads nevertheless to consider the qualitative aspect, even if this would mean a re-appraisal of the holistic principle.

Therefore we have to consider the mechanism(s) of evolution gradually developed through the ideas of Buffon *c.s.*, Lamarck, Hutton, Malthus, Lyell, and finally synthesized by Darwin & Wallace, by whom the gradually grown idea of adaptation was more closely defined as adaptation caused by selection on the basis of competition, more popularly explained as survival of the fittest.

Competition, resulting in selection, must of course have been a powerful agent through the history of life. It is supposed to have been already present on the abiotic level. Probably already at this stage was it effective, with the understanding that 'decisions' were made resulting in a restricted number of initial organic compounds (see Quispel, 1968). The same principle of competition is held responsible for the evolution at the akaryotic and later karyotic stages at the biotic level. It is clear that competition results in restriction of the pre-existing variability, either by adapting the mechanism of segregation or by preferential elimination of less adapted individuals.

In these early stages, again, 'decisions' were made about basic features of structure which became the matrix of later evolution. One may well imagine that, if 'decisions' had materialized in different ways, other matrix structures would have originated. Thus, the impact of these early competitions must have contained a very important factor of chance. Chance is in this context of course to be understood as causal, but it includes the possibility that matrix structures of genomes could have been different. The early 'decisions' made, must thus have had a decisive, hence restrictive influence on later evolutionary lines for further development. Once a stable basic matrix pattern of genome design was established, the fate of further evolution based on this design was curbed, the stakes of its potential boundary being set out, comparable to 'evolution' of basic designs in industrial tool and machine development.

This implies that only part of the potentially possible organic structures really have got into actual existence as viable living organisms. We cannot fathom what other basic designs could have had viability, and so, questioning what percentage of the total potentiality of living matter was ever realized, becomes an impossible and useless exercise.

The main basic design for plant evolution must have been the unicellular algae and bacteria*, probably soon followed by fungi. They must have been capable of conquering the earth, as they still do. They coupled plasticity against environmental factors with diversification, resulting in the occupation of all niches, as they still do. This diversification consisted of the origin of species adapted to the environmental niches of an unimaginable variety: freshwater, seawater to brine, arctic to tropical conditions, rock faces and snow, even extremely high water temperatures. It seems doubtful whether this can be explained or that it needs to be explained by the competition/selection axiom; the world was bare and niches unoccupied, it was free for all.

Our unique planet once occupied by bacteria and algae, we are confronted with the question why there was any ecological or adaptational need or necessity for evolution to more complicated organisms according to the competition/selection axiom as the mechanism of evolution.

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* I have always been surprised that virus is usually advanced as more primitive living matter, due to a more simple design. Since virus is inert matter, only capable of multiplication as a parasite in the protoplasm of more complicated real organisms, they cannot have preceded, or be ancestral to, the latter.

It is likely that the unicells were followed by thread-like, branched and foliar algae, which also needed space. They may have locally shaded out, but not replaced all the unicells. They were received as affiliated newcomers, to belong to one happy family. Under favourable environmental conditions there is no end to the extension of the family, as is e.g. shown by the tropical rainforest, the flora of the Cape or of New Caledonia or Western Australia which are not only very rich, but where also each family and each genus is represented by many species thriving peacefully together.

Here we glimpse a first difference, the passive tolerance of plants as compared with animals. Plants are tolerant living beings, they do not eat their close allies, they do not hunt and kill in order to survive, they do not need all sorts of devices towards upmanship in order to live. This passive tolerance, lack of active aggression, suffering in silence, subdued happy-go-lucky mode of living, just waiting what will happen, this inertia as compared with animals, is characteristic of plants. To no mean degree this is due to the sedentary bond with the terrestrial substratum.

Animals show generally motility, they show aggression, they are out to exterminate rivals, show competition and intolerance, and are for a great deal not sedentary and bound to the substratum, but move around. It should be mentioned that among the most highly evolved animals, *viz.* birds and mammals, there are striking examples of tolerance within the species, mutual aid, and even birth control by various sophisticated devices. Still, these are exceptions, and especially tolerance towards the members of other species is very rare.

These two opposite tendencies, passivity and activity, must, I believe, have the important corollary, that animals are under greater pressure to develop steadily more complicated means and ways, including structures in order to keep up with competition and have to use all possible advantages, which by mutation occur, in order to survive. Their structure becomes in this way adapted to competition, leaving hardly room for organs or other features which are useless or irrelevant to survival. Their organization is thus changing rather rapidly; organs once useful have been superseded by others and though they often do not disappear entirely, they soon are hidden away and can only by careful comparative anatomy be traced as insignificant vestiges.

Thus I believe that, while the competition/selection axiom is valid for animal life, plants behave more conservatively, as they do not suffer from similar pressure. They develop more slowly and give free way to inventiveness in forms and structures which are irrelevant to competition/selection, creating features which sometimes are called adaptively-neutral.

It should be noted of course, that rudimentation in flowering plants, due to saprophytism, parasitism, or secondary aquatic life, is comparable to rudimentation in animals. Nevertheless, it seems to be less stringent in general, and it seems to proceed much more slowly.

Competition and survival in plants is passive; it is mainly caused by or directed against the inanimate environment, heat and cold, drought and water, seasonal desiccation, exceptional soil types, and presence of toxic minerals, etc. A few exceptional cases of allelopathic behaviour mean only that certain plants may not tolerate others in their immediate vicinity, but there is plenty of room for them elsewhere. Besides, allelopathy does not concern competition between allied species, but rather implies an influence of exudates of non-related species. Parasitic plants may destroy or harm their hosts, but they usually come to a balance agreeable to the survival of both host and parasite, sometimes even to a parasitical symbiosis (*Rafflesia, Balanophora,* etc.). In their strife for light plants may shade out others, but there are always open places where the shade-giving plants cannot thrive and have to give way to the smaller ones.

There is no case known to me that a so-called better adapted plant completely outrooted another allied species. It has been shown that seedlings of one species may have an advantage over those of an other in experiments, but I doubt whether these experimental conditions can be applied to germination in nature, and if it were so, in nature it will always turn out to be a mere question of proportional abundance, not of extinction through competition. This can hardly be otherwise, as each plant species has its own ecology, including resulting abundance: no two species have exactly the same ecology. To be precise, and to quote a simple example: very few closely allied species of plants will be able to survive in a peat bog of high acidity, or in soils loaded with heavy metal ions, but we never observe that one species eliminates all others.

In conclusion, it appears that intra- and inter-specific competition as well as natural selection (in the sense of elimination of weak individuals by stronger ones) among plants is insignificant. The occurrence and abundance of plants is almost entirely defined by environmental factors.

Against animals in search for food, the plants behave passively. Many may contain poisonous substances, or elaborate structural devices which seem to be effective in keeping off some of the potential predators, but even in these cases it is the animals which adapt themselves; as a matter of fact the most toxic plants have animals which feed on them. Thus, it is essentially a question of equilibrium, based on mutual adaptation.

Animals on the other hand have the problem of surviving two kinds of struggle for life. The first struggle is the same as that of plants, against the inanimate environment, but the second is against each other. Instead of the basic autotrophy of plants there is a food chain in animals, often very complicated, in which besides plants other animals take part. This dual struggle means a high degree of competition among animals, and thus a much higher pressure towards upmanship. This must inevitably lead to more rapid change and development, that is, evolution.

A third point is that the number of niches for animals is much greater than for plants, and far more finely knit, enabling them to develop through the pressure of competition/selection an immensely greater display of form-development and specializations.

A fourth, though minor, point is that animals can occupy certain environments unfit for plants, such as the depths of the oceans, the atmosphere, caves, etc.

Concluding, this concise discussion may serve to explain the observation Hooker made, that the variety in the animal kingdom is far greater than that in the plant kingdom.

What is more important, it throws also doubt on the holistic view of evolution in animate nature, in particular on the intensity of competition in the struggle for survival.

2. Survival level and Patio Ludens

The views exposed in the introduction lead to certain consequences which I have alluded to in my essay on plant speciation in Malesia (1969), *viz.* that there is a difference in the situation of the survival level in plants as compared with animals. I have illustrated this in a generalized schematic figure (Fig. 1).

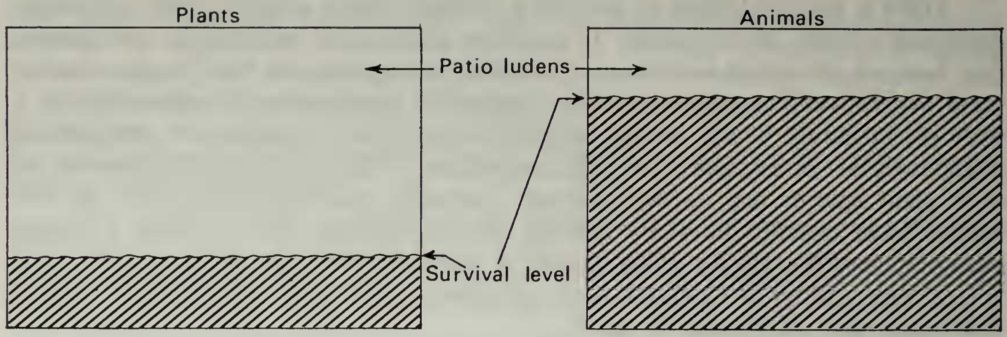

Fig. 1. For explanation see the text.

The rectangles represent the total potential space for structural development, in conjunction with the degree of the minimum requirements necessary for survival, indicated by the hatched space. The demarcation is marked by a line, which I call the 'survival level'; beneath it one has to think of all structures and functions compulsory for survival.

Above the survival level there is '*patio ludens*', represented by the blank space which can be occupied — but will not always be necessarily fully occupied — by structures which are irrelevant to survival, hence fall beyond competition, selection, and adaptation.

Through the more intense competition and more complicated life of animals, I believe that *patio ludens* is for animal life only a narrow zone as structural development is under high pressure of competition/selection, and development is more acutely directed towards trying to employ and adapt any new feature which it can use for its survival. The survival level in animals lies thus considerably higher. It should be admitted though, that adaptive-neutral features have occurred in animals as well, at very primitive levels, e.g. when the divergence started in arthropods into the insect and arachnid phyla, but also at the level of speciation, as exemplified e.g. by protuberances (often allometric in behaviour) in protozoans, arthropods, vertebrates, etc. See p. 112. Also I would not exclude the possibility of a lower survival level in primitive groups of animals.

In plants the survival level must generally lie much lower and primary structure equipment is more primitive. There is no such competitional strife in perfection of adaptive structures as among animals. Consequently there is ample allowance for the possibility of structural features (form development) which are irrelevant to competition and adaptation.

These irrelevant or adaptatively neutral characters in plants concern both gross morphological characters and internal characters. It is for a woody plant not a matter of competition whether it develops into a tree or liana or a scrambler; or whether a liana twines to the right or to the left. Phyllotaxis seems also a quite irrelevant character, all types are equally well fit to let a plant live and survive. Presence or absence of stipules can equally not be attributed to have special function for survival. To prevent any misunderstanding: functional adaptations are very important, but they are not in any way restricted by neutral basic features like e.g. phyllotaxis.

Merousness of flowers also seems a matter of chance choice. Thus it would be a far-fetched idea to postulate that 5- or 4-merous flowers have a competitive value, the one better than the other, or 3-merous ones over 2-merous flowers (cf. also Bateson, 1894: 67). Monocotyledons are characterized by 3-merous flowers, but 2-merous ones do equally well (*Stemona, Paris,* etc.).

In the flower the number and position of anthers, obdiplostemony, etc. is an often systematically very constant structure, but it seems futile to ascribe competition value to such structures. In a very uniform genus, such as *Tristania*, the number ranges from 5 to very many (and then in phalanges); in Borneo many species grow together and none of them is crowding out the others.

As to gynoecium, its position: superior or inferior, its merousness, the position of ovules, erect or pendent, axial or parietal, seems not to have any bearing on competition. It just happens that in families like Theaceae one or a few have by exception an inferior ovary (*Anneslea*) and in Rubiaceae some have a superior ovary (*Gaertnera*). Or this may vary even within one genus (*Mastixiodendron*). A similar situation prevails with the seed. It could not be argued with good reason that the presence of two cotyledons would be of any competitive value above the presence of one cotyledon, or for that matter of more than two. The same holds for the place where reserve food is stored, in the cotyledons or in albumen, or in both, or whether seeds are large or small. They all come up equally well ecologically. As a matter of fact any systematic structure (systematic character) may be constant in one group and vary in an other; properly none of them have absolute value.

In this context it is noteworthy what A. C. Smith remarked, when he spoke of the phylogenetic systematy of the Monimiaceae (1973: 55): "The basic complex with which we are here concerned, within the Ranales, is characterized by having comparatively primitive xylem, ethereal oil cells, monocolpate pollen or pollen derived from that type, and unilacunar nodes. Incidentally, these are not glaringly apparent characters, but they are some of the basic characters that taxonomists concerned with Angiosperm evolution must use if they seek to understand (phylogenetic) relationships".

In all these structures plants do not compete, their only concern is to stand certain primary minimum conditions under the survival level.

Concluding, it must be well understood as a major point that it is precisely these 'technical characters' which serve for the schemes of the evolutionary system of the Angiosperms, that is, that they reflect phylogenetic affinity and are employed for the reconstruction of their ancestral relations and derivation. Though these structures have no adaptive value, the way of evolution is traced by them. And this shows their importance.

Anatomical features and structural fitness of Gymnosperms

Even for anatomical features the evidence that complicated, specialized structures would have originated as a result of competition/selection to enhance their functional value, is dubious, if we try to measure their success.

One might imagine that vessels for transport of water, assimilates and minerals would mean a great advantage over tracheids. This rough assumption is, however, not borne out by the facts, as among both groups are the highest trees known to exist, and the oldest in life-span are even among those without vessels. Furthermore, it is not so that among the vesselless trees growth need to be hampered by absence of vessels and thus growth would be slower. Saplings of certain conifers may show a very rapid upgrowth indeed, comparing favourably with that in eucalypts. Conversely it is not so that saplings or trees with vessels always show a rapid upgrowth; some grow extremely slowly. This whole matter is dependent on several factors, sometimes individually on soil and climate conditions, and structure and capacity of root system, but mainly on the ecological capacity of the different tree species of each group, irrelevant of presence or absence of vessels.

A conclusion is sometimes made about the better adaptation by presence of vessels with reference to the palaeontological experience that Gymnosperms have very gradually been partly replaced by Angiosperms, in the sense that terrestrial space now occupied by Angiosperms was in pre-Cretaceous time the domain of Gymnosperms. This is certainly true, but it is doubtful whether this generality can be explained by improved 'adaptive values'. On the one hand it should be remarked that anatomically and functionally the Jurassic *Ginkgo* was obviously a success, but similar things can be said of *Araucaria, Metasequoia*, Cycadaceae, and others. On the other hand trees equipped with Angiosperm-type wood from the Cretaceous had also to make place for newcomers. In addition it should be remarked that anatomists tell us that various anatomical features seem to be without function. Finally, the 'decline' of Gymnosperms is, I feel, slightly exaggerated; they are still responsible for a high percentage of all organic matter produced on our globe. This idea of 'decline' may, possibly in part be due to the proportionally low form-development which is indeed negligible if compared with the enormous diversity in structural development of Angiosperms.

But this is altogether another matter than inadequacy or deficiency of structural and functional fitness. This matter belongs to the question one can also put for structural development of many phyla and groups: why some are ancient but remained small and others grew to great diversified groups. Even in the Mezozoic the Gymnosperms as to number of genera and species were probably always fewer in number than the Angiosperms are today. The only guess one can make in this obscure field of speculation is that the basic genome pattern of groups remaining small was 'rigid' and did not allow for abundant form-development, and that the genome pattern of so-called more successful groups or phyla was more suitable or 'versatile' and had the promise of more potentialities. Similarly as in chemistry certain atoms (for example C, Si, etc.) have more potentialities as the basis of compounds than others: or in terms of plants, certain species appear to be fit to be 'developed' into a large number of edible or ornamental variations, while others simply resist this and do not possess genome potentialities fit to be exploited by domestication.

In chemistry potentialities of chemical evolution — in the sense of capacity of producing compounds — can be foretold. This should then also be possible for the chemical compound named genome-structure. But this is so complicated that it will never be possible to compute why the pattern in the Linaceous genus *Ctenolophon*, which existed already in the Upper Cretaceous, persisted all the time in the tropical forests (now extinct in the neotropics) but produced at most three species, while the obviously much later evolved Compositae, Acanthaceae, etc. showed an astounding diversification though they are structurally very homogeneous from the taxonomic point of view.

I may mention a few other examples of old genera which are known from the Upper Cretaceous or Palaeocene which have never evolved into large groups, e.g. *Pachysandra, Nypa, Knightia,* and *Gingko;* contrasting these with *Ilex, Quercus, Nothofagus, Alnus, Symplocos*, etc., we cannot account for the latter's successful development, taxonomically and geographically.

I do not believe that it will ever be possible to compute the causality of structural development or account for the potentialities of the genome matrices and show that it could not have been otherwise and could be foreseen, or at least expected.

I have stressed (1969) that a congenial, equable climate, such as the tropical rain forest, which has persisted ecologically unhampered for aeons, has the lowest competition pressure, hence the lowest survival level in all habitats for plants, hence for them the widest *patio ludens*. Consequently the tropical rain forest offered the longest and largest opportunity towards form creation on the globe, for all kinds of structural developments which came up to survival conditions. It became the cradle of the development of Angiosperms as well as many other groups of the plant kingdom. This is also the reason why the tropical flora contains so many isolated genera and, besides, the frame-work of all larger families, which swarmed out later to other parts of the globe.

3. **Pre-adaptations in plants**

This term has sometimes been loosely applied in an evolutionary sense, to explain for example the structure of seeds and fruits on the sandy beach.

These fruits and/or seeds, which are all provided with some buoyancy device, are either hard-shelled, or have their seed surrounded by a stone and/or fibrous tissue and thus protected against the surf and grinding on sand, rock, coral and pebbles. But it must be kept in view that the representatives of the beach and the tropical beach-forest are just single or very few beach-specialized species of large inland genera which all display the same fruit-seed structure in inland vegetation, whether it be the hard-shelled Leguminosae (*Caesalpinia, Canavalia, Desmodium, Erythrina, Pongamia, Sophora*) or species of for instance the genera *Barringtonia, Calophyllum, Casuarina, Clerodendrum, Colubrina, Cordia, Cycas, Cyperus, Dodonaea, Euphorbia, Fimbristylis, Guettarda, Hernandia, Hibiscus, Ipomoea, Ischaemum, Morinda, Pandanus, Scaevola, Spilanthes, Terminalia, Tournefortia, Wedelia,* etc.

To bring their morphological capacities in conjunction with adaptation, as so-called 'pre-adaptation', seems to me a serious misleading of evolutionary thought, as it suggests the childish idea of pre-sighting on the part of the plants that it might be useful to develop such structures, just in case it might be helpful to cope with the exigency of sharing the future life of a beach-comber. These structures were already there in the genera and have nothing to do with the axiom of competition/selection pressure. Invading the beach just meant for these genera invading new terrain, in part unoccupied. The effort often was not even considerable, as they remained for their root system largely freshwater plants, and for several genera the hot beach conditions did not differ much from their main development in dry inland savannahs.

I could for many other specialized habitats give a similar picture, in the way that so-called pre-adaptations were already represented in existing structures outside these specialized habitats. A development of large hypocotyls with food-reserve in the seed, is for example represented in many tropical inland trees; it developed strongly in the littoral Rhizophoraceae, but certainly not as a result of competition/selection pressure. In passing: this feature is also not necessary at all, as the tiny seed of *Sonneratia* mangrove trees does not show anything of the kind.

A similar picture is displayed in almost all ecological specializations, be it rheophytes, therophytes, etc.

It should be added that, whereas the survival level scheme holds for one species or group at one time and in one place, the corollary is that *patio ludens* characters may, in later stages, or during migration of a taxon to other places with different environments be 'pushed down' under the survival level as they become essential for survival in these stages or places where their latent existence is activated. Such characters may be physio-ecological as well as morphological.

In conclusion: (1) structures originate and may suit more than one ecological class or niche, necessarily leading to the peopling of specialized habitats with an array of unrelated, 'generic waifs' coming up to the minimum requirements of the habitat.

(2) 'Pre-adaptation' is often used in a misleading way, as a fancy term invented through pre-occupied thought. It should be defined more clearly, as in most instances in plants it has nothing to do with adaptation. It should preferably be replaced by the neutral term: 'pre-disposed structure'.

4. **Early differentiation**

The survival level scheme set out in fig. 1 is, of course, meant for one time of each plant or animal in one place: it is dynamic, because in the course of time the significance of characters will, or at least may change. Structural characters as they appear today to belong to a rigid scheme may, in the far past, in primitive ancestors not have had the organizational significance they have now. Such characters may have been then irrelevant not only in plants but also in animals, because the more primitive the organisms are the lower is their survival level and the larger their *patio ludens* must have been.

I have in this context questioned zoologists in asking why in the great phylum of Arthropoda the Insecta are based on an organization scheme with 6 feet, while the Arachnoidea are based on a scheme with 8 feet, and whether they assume that such a basic structure has been the result of competition and natural selection; their answer was in the negative. Similar questions can be asked about the fact that Vertebrates all have 4 extremities, Cephalopods have either 8 or 10 arms, that the basic scheme of Echinodermata is 5-merous (in an exceptional small group 'running wild' towards an 11-merous structure) and why this would have advantage over a 3-, 4-, or 6-merous structural scheme which would equally have been feasible. In corals, on the other hand, there are again two large classes, the Octocorallia and Hexacorallia; why are there no Pentacorallia? With the exception perhaps of the quadrupedal organization which may be the most 'economical' solution from the structural point of view as well as for neuro-locomotor organization, these numbers like many others in animals (e.g. 5 fingers in tetrapods, 21 scleral elements in sauropsids) and like merousness in flowers, appear to be quite accidental and devoid of adaptive or selective significance. These structural schemes must have been fixed at initial stages, but the agency which caused the 'decision' seems very obscure. Still this decision was extremely important, being decisive for later phylogenetic organization.

It seems a far-fetched idea that this decision had anything to do with competition/selection; to me it appears a matter of casual structural development for which the potential was already embedded in the basic genome matrix. Once triggered development could not proceed otherwise.

In the initial primitive stage these basic structures may well have been *patio ludens* characters of the group concerned, irrelevant of competition/selection pressure, similar as must have been the case with many phylogenetic characters of plants, as has been advanced earlier in the preceding chapter.

This leads then to consider the genetical status of the merousness, and to the question: were these characters which have now class or phylum value at the early initial stage of much lower genetical value and apt to variation, maybe even at species level? How could it then be understood in the genetical sense that, what initially was possibly defined by a few genes could later develop into a strictly fixed bond characteristic of a whole phylum, and obviously so essentially integrated in its genome structure that it was not liable to be influenced by later mutations? In fact, except for rudimentation, secondary changes of such accidentally fixed primitive numbers are very rare indeed.

5. Saltatory evolution in plants

It is axiomatic that structural development is always proceeding stepwise, never completely gradual. In this point there can be no difference in inanimate or animate chemical compounds: both energy and matter are discontinous, 'molecular': quanta, atoms, genes, and so their changes must be discontinuous.

The changes brought about by evolution in organisms can of course be small or large; if the steps are very small, the process looks to us gradual and one can speak of 'gliding evolution'; a mutation concerns at least one gene change. But if the changes are larger steps, one speaks of saltatory changes and development.

As in animals evolution in plants starts with divergence, and divergence must start from diversity, often called variability, of a genetical nature.

The first major step to evolution is speciation, that is, changes on the species level. This holds for all levels, as the first representative of the suprageneric taxa must also belong to a species. The origin of species is thus the most important phenomenon in evolution. But what is the criterion for a species, especially its delimitation? In two previous essays (1949, 1957) I have extensively treated the causes of variability and species delimitation respectively. I have come to the conclusion that there are essentially two ways of speciation, *viz.* through racial segregation and through saltation.

With racial segregation a species population segregates in the course of the slow process of dispersion into spatially (ecologically or geographically) isolated (replacing = vicarious genetically differentiated ecotypes, races and subspecies, in response to the ecological environments in the new lands (see van Steenis, 1949: xliv—l, and 1957: clxxxiii—cxcvi).

Such raciation may finally result into a compound string or array of 'beads' representing *convivia* in Danser's sense.

Such races differ from one another in their gene combinations, but these differences usually concern only a restricted number of genes and in the intervening border zone where two adjoining races meet there is a transition zone where fertile hybridization takes place and intermediary specimens occur. On the borders marginal differentiation takes place by pioneer advances (genetic drift).

The general experience in plants is that raciated species populations form together one *commiscuum* (*syngameon* of Lotsy) in Danser's sense (1929). Such a *commiscuum* is really a net of interfertility, as all races are miscible with the adjoining ones. Even if widely spaced races may become isolated through circumstances, fertility usually remains intact. There are many cases to support this. For instance the Pleistocene glacial period has broken up many populations, but through this cause now widely disjunct 'species' of, for example, *Platanus and Campsis,* in East Asia and America are still miscible; properly they should be treated as races of one species population and classified taxonomically as subspecies.

The possibility that the furthest remote races have accumulated so many hereditary differences that they prove incompatible if brought artificially into contact cannot be excluded. They may still be crossable but not miscible any more, that is, in hybridization will not go beyond the sterile F_1 hybrid.

I would not go so far as to exclude the possibility that accumulating differences in gene composition may, after a long period of isolation, in a restricted number of cases lead to new species. This possibility is still more likely if partial populations survive in isolation on islands.

But the general impression is that in plants speciation through racial segregation must be a rare phenomenon and that this so-called 'micro-evolution', however interesting it may be for an understanding of the variability within a species is, in plants, of little significance in phylogenetic evolution. Racial segregation is a restricting agency, pruning variability; it is in phylogenetical sense not a creative agency. Goldschmidt (1933) defined this in saying concisely: "Geographische Variation ist weder eine Vorstufe noch ein Modell des Artbildungsvorganges".

Saltatory evolution appears, on the other hand, to be the common way in which form-making in plants takes place, and this can easily be observed from the still growing, important body of facts about chromosome numbers. Scanning these it is obvious that a very large number of species are polyploids, either autoploids or alloploids. Still more interesting is the fact that this increasing information shows within families the frequent occurrence of dysploid, aneuploid and allopolyploid numbers which are not seldom characteristic of genera of higher taxa. Genera can have allopolyploid genomes, as occurs e.g. in *Gossypium.*

Cultivated cotton is generally tetraploid (52 chromosomes), and is supposed to be an allotetraploid of *Gossypium arboreum* L. x *G. thurberi* Tod. (or some other Asian and American diploid species) (Brown, 1951). Note that the cultivated types are natural allotetraploids and that they behave as diploids. The product *arboreum* x *thurberi* is not quite similar.

Stebbins (1971: 179-201) emphasized the important creative role of polyploidy in Angiosperm phylogeny and concluded (*l.c.*: 198) that "extensive polyploidy must have taken place during the early evolution of woody Angiosperms. The most probable hypothesis, therefore, is that the polyploidy which gave rise to the basic numbers of woody plants took place at various times during the Cretaceous and the earliest part of the Tertiary Period, while the diversification of species on the basis of secondary basic numbers is largely a product of the Tertiary and Quaternary periods". He cited many examples of tropical taxa in this context and estimated that between one-fourth to one-third of the flowering plants are polyploid with reference to their nearest relatives.

In some families taxonomic affinities can thus be supported cytogeographically and attempts can be made towards a reasonable reconstruction. See for instance the most interesting papers on Australian Proteaceae by Johnson & Briggs (1963), on *Pomoideae* by Challice (1974), on the Casuarinaceae by Barlow (1959), the Loranthaceae by Barlow & Wiens (1971), the Oleaceae by Briggs (1970), and the Malvaceae by Bates (1968).

There are at least two processes by which chromosome changes are brought about, *viz.* hybridization (proved in many cases) and obviously irregularities in meiosis (translocation or 'centric fusion and fission', aneuploidy, duplication); there may be others.

The main point is, that major genomic rearrangements of the type quoted above, occur in a single generation, indubitable proof that saltatory form-making has been the major feature in plant evolution. See fig. 2.

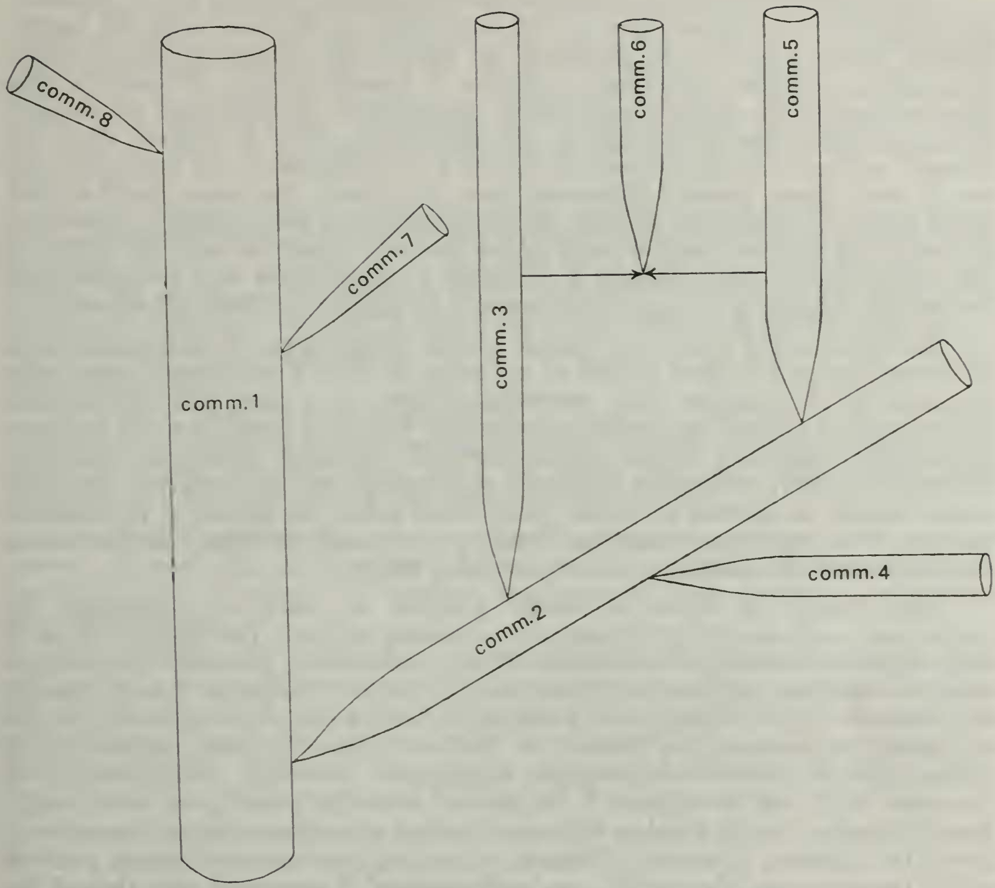

Fig. 2. Scheme of saltatory evolution in plants by individuals.

Commiscuum 1 has produced the daughter *commiscua 2, 7,* and *8*. *Commiscuum 2* has produced the daughter commiscua *3, 4, and 5.*

Commiscua 1, 7, and *8* show mutual affinity and so do *commiscua 2, 3, 4.*

Commiscuum 6 is an allopolyploid between *commiscua 3* and *5;* it shows affinity with several other *commiscua* but is also an example of reticulate phylogeny.

Even though they may not become established at once, they certainly re-occur with a given probability and sooner or later will result in a population of individuals with novel characteristics. Thus, the idea seems justified that evolution in plants is largely of a saltatory type. For instance, polyploidy undoubtedly has been instrumental in many cases, in producing new forms. Some botanists claim that autopolyploids are side-products of evolution, being variations on a given level only, whereas evolutionary progress occurs on the diploid level. There is on the other hand no doubt that amphidiploid combinations are significant in evolution. More importantly, saltatory genomic changes in the diploid range are well-documented, especially in the genus *Clarkia* (Lewis, 1953).

In any case it appears that such evolutionary changes have nothing to do with competition pressure or selection of the fittests.

Naturally, the fit survives, the new plant arisen must come up to survival level and be able to germinate, grow, and propagate, but that is all there is to it, harmless extras are allowed.

It is admitted that not all families show an important array of ploidy variation, e.g. Pinaceae or Lauraceae seem to be exceptions. In the Lauraceae the family number seems to be x = 12, including the vegetatively aberrant parasitic, herbaceous genus *Cassytha,* according to Okada & Tanaka (1975). Incidentally, this number seems to be common in primitive Angiosperms. In such cases the number of chromosomes does not tell much, and information would be needed about the internal structure (chemical composition) of the chromosomes and also about the way in which these 'internal' differences have come about. The same should be said about genera in which the number of chromosomes is very constant; sometimes differences in size and shape already reveal this in a superficial way. The study of the genome architecture in plants is of course a most difficult field to explore and we are only beginning to enter it, for instance by measuring DNA hybridization.

Finally I would here also remark on the phenomena of teratological and neotenous forms, for which I refer to my essay of 1969. Teratological forms arise as sports all of a sudden. With teratological forms it is clear that physiological chain-reactions in plants have undergone change. Classes of terata so much resemble taxonomical characters (prolification, antholysis, enations, cohesions, fasciation, laciniation, adesmy, reduction, petaloidy, scyphogeny, and ceratomania) that they cannot simply be ignored or waved away. Some terata are known to be inherited and due to a single gene mutation. Bringing terata and phylogeny in line means that they should be hereditary (see e.g. Stubbe, 1966).

The concept of terata is mostly accepted as something 'abnormal' or 'monstrous', and should be disposed of as meaning inferior. This appears to me a very superficial, emotional evaluation. Many evolutionary processes are brought about by reduction, suppression, fusion, etc.: a panicle of separate flowers changes into a head or fig, or is reduced to a raceme, or even a single flower; meristems are suppressed and contraction follows; or they are joined to other meristems and fusion follows (ovaries of *Morinda;* epiphyllous flowering; concaulescence in *Solanum,* etc.); leaf production is suppressed on twigs which grow into thorns: lateral branches do not develop inflorescences and are metamorphosed into curved hooks for climbing (*Uncaria*). There is no end to these metamorphoses, each of which represents an 'abnormality' or 'malformation' if compared with that of the immediate ancestor which did not possess the new structure. Thus the 'concept' of terata has a very definite structural meaning in biology, *viz.* a sudden change of structure which differs from the taxon from which it evolved.

Comparing trees of the *Naucleeae* with the miserable *Uncaria,* a climbing plant, of which part of the flower-bearing side-branches are flowerless and deformed into curved hooks, the latter is an abnormality; but surely *Uncaria* has found its niche, proved its vitality and developed into quite a large genus. Considered unemotionally from a broad outlook, systematical teratologies are really hereditary teratologies.

Many of these changes are morphological reductions or suppressions, and that stamps them to belong to neotenous behaviour, that is: reaching maturity before all parts have developed as in the immediate ancestral form. Precocious flowering may turn a woody plant into a herb; precociously flowering herbs may be reduced to flower production on the cotyledons of the seedling (*Monophyllaea*).

For plant evolution I ascribe (1949, 1969) great importance to neoteny which I regard as one of the two crucial processes in their evolution. Takhtajan (1954) spoke of 'phylogenetic teratology' and correctly generalized and applied it to all contractions and reductions, as a vital element in form-making.

Systematical teratologies originated in all probability suddenly as saltations, in one or more steps and survived if they were viable in the sense that their ecological and reproductive capacity reached survival value, with their morphological caprices tolerated.

In contrast with the chromosome 'mutations' caused by hybridization or other mutative changes I have the conviction that important changes in morphogenesis might often have been caused by not too integral genetical changes. I derive this from the fact that fasciation (as in *Celosia cristata* L.) or pelorial flowers (as occur in Scrophulariaceae, Orchidaceae, etc.), which give a fundamental change to structure, seem to be based on presence or absence of one or very few vital genes only.

I once discussed with a famous botanist how he thought that a pitcher of *Nepenthes* might have originated. To my surprise he said that this might have been gradually built up, may be by a thousand gene mutations. Obviously he was ignorant of scyphogenous structures in the cultivated 'crotons', fancy varieties of *Codiaeum variegatum* (L.) Bl., in which the rough skeleton of a *Nepenthes* pitcher can be observed, the blade, tendril (naked midrib) and at the end a pitcher with an appendage (the lid).

If such a structure can be formed in a 'sport' of one known species, little imagination is necessary to assume the origin of a pitcher, through scyphogenous action, in a few saltatory steps. Once the initial step was made, autonomous perfection can be imagined in a few more orthogenetic steps.

Blocking of certain vital genes by mutation may cause development to follow another physiological pathway in the chain-processes leading to morphogenesis and production or reduction of proteins, hormones or other substances controlling form-development.

I have talked about this matter with geneticists, both on the matter of stability of structure and obviously responsible genome patterns on one hand, and sudden changes in a few vital genes on the other hand, but it seems that these seemingly contradictory phenomena cannot easily be translated in genetical terms of molecular biology. They find this a most complicated matter about which even generalized ideas of morphogenesis in genetical terms can not yet be given.

However unfortunate this may be, I hope the meaning of the arguments given above is clear. They lead to the following conclusions:

(i) In both major causes of evolution of plants, that is either changes in the gross chromosomal patterns (allopolyploidy, dysploidy, aneuploidy) or the physiological function changes of morphogenesis by neoteny, the changes are sudden, saltatory.

(ii) The saltatory steps are at least at species level, but higher categories, for instance genus level, may also be involved.

(iii) The conclusions given above imply that evolution of plant structure is essentially not caused by competition but is an autonomous process in which chance plays a distinct rôle.

(iv) For form-making the gradual accumulation of gene changes resulting into raciation may not be excluded as a cause of segregation of species but should be considered as of minor importance, while also their competition is not the overwhelming agency as frequently supposed.

In fig. 2 I have drawn a scheme reflecting the above considerations.

6. **Gliding evolution in animals**

As explained in the introduction the mechanism of evolution in animals must be much more complicated than in plants, as in addition to autonomous development in *patio ludens* at early stages it must include competition. As in most plants raciation in species populations easily occurs, sympatric and allopatric, the main difference with plants being that such raciation is largely a matter of competition partially for food and shelter, but with the additional agency of sexual selection, which is absent in plants. Through these combined factors and competition racial segregation will in animals usually develop more rapidly than in plants. By this sexual selection partial populations drift apart and become in the practical sense incompatible, and thus a start is given to divergent development. In several cases it has been shown experimentally by artificial insemination that recognized good species of insects, which in nature keep strictly apart, are factually compatible. But through their isolation by sexual selection and then occupation of a specialized ecological niche they will finally drift apart, by populations, to such degree that they become incompatible genetically. Thus they start as *convivia* but gradually become *commiscua* and finally *comparia*, to stand on their own for future development. Mutations irrelevant to survival will be possible, but these will play a much smaller rôle than in plants as *patio ludens* in animals allows for much less free form development than in plants by predominant competition and sexual selection pressure: any new feature arising is 'tested' on its usefulness for competition. See fig. 3. The reader may recall that a prominent zoologist and geneticist, R. Goldschmidt, has put forward the idea that in the macro-evolution of animals, saltatory re-arrangements of the genome, and 'teratological' mutations "the hopeful monster") have been important. But there seems to be little evidence to support this concept.

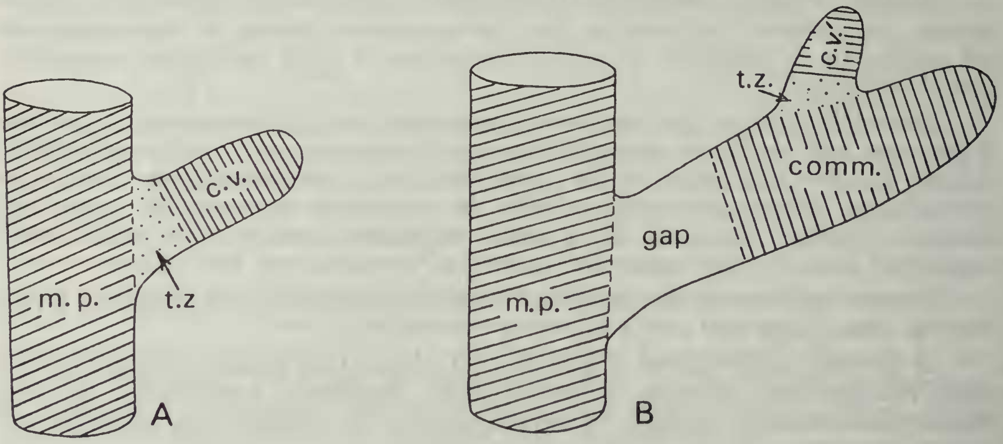

Fig. 3. Scheme of two initial stages of divergence in the gliding evolution of animals by populations.

A. A mother population (*m.p.*) starts to form a *convivium* (*c.v.*); it is still loosely connected and compatible with the mother population by a transition zone (*t.z.*) of rare miscibility.

B. In a further stage the *convivium* of fig. A has developed into a new independent *commiscuum* (*comm.*) which has become incompatible (indicated by a 'gap') with the mother population (*m.p.*). This new *commiscuum* is undergoing in its turn a similar differentiation and has formed a new *convivium* (*c.v.'*) comparable to the scheme in fig. A.

The main conclusions on the differences of animal evolution as compared with plants appear to be fourfold:

(i) Evolution in animals will be gradual, through accumulation of competition/selection characters by 'gliding evolution', through separation of divergent populations, raciation with practical incomptability into *convivia* which gradually develop into truly incompatible *commiscua*, and finally into *comparia*.

(ii) Evolution of animals goes in general by populations and not by individual specimens as usual in plants.

(iii) There is little opportunity for *patio ludens* characters to develop, as all are tested on usefulness for competition and survival, and are subject to sexual selection which is unknown in plants.

(iv) Saltatory steps are not excluded, but they must be extremely rare in proportion to their frequent occurrence in plants.

In fig. 3 a scheme has been drawn reflecting these considerations.

7. Co-evolution of animals and plants

As I have emphasized in the first chapter plants were the first organisms of all organic evolution by their capacity of assimilation, capturing and storing energy. Animal life developed later, and never became independent. Food chains always have to go back on plant life.

Animals could in a broad sense be considered to lead a parasitic life; they browse and feed on plants which make their life possible.

Except for negligible exceptions plants play the passive rôle, and the organic matter they produce is at the disposal of animals which are specialized for taking advantage of anything they can find, even the most indigestible organic products. From this follows that plant evolution goes independent of animal evolution and that novelties arising in plants are secondarily exploited by animals. Notable exception: a large part of Angiosperm evolution has been aligned to pollination 'symbiosis' with animals.

Apart from the plant bodies themselves, used as food, animals are attracted to them by colours, scents, and obvious shelter. Evolutionists seem generally to assume that glands, floral and extra-floral, give competitive advantage to plants through the prowling animals. They have theorized that in such a way the competition/selection principle was forced on the plants, inducing plants to excrete more nectar or other substances, and thus induce numerical advantage over those which produced less, or less abundant, attraction to animals.

This is a very crucial problem indeed, and it seems difficult to prove or to disprove whether the assumption of this advantage is true or not, and that it worked under natural conditions.

For one thing, experiments lack of course the factor time. Even if it were proved that there was advantage to plants by animals this would mean that this assumed advantage would result into greater numbers of the plants (higher population density) which had the advantage. It is hard to believe, however, that this would mean extinction of those which offered less benefit. The latter would have a lower population density, but we can observe that precisely such a phenomenon is ubiquitous in the plant kingdom. In each genus certain species are rarer than others, but it would be a far-fetched idea that all the rare or rarer ones are nearer to, or nearing extinction. This is largely a matter of ecology, available niches, etc., not an immediate result of competition pressure: each species has its own ecology, including frequency of occurrence.

For another thing experiments never reflect the situation in nature. Imagine an experiment in which seeds of two allied species were sown together with the result that the seedlings of the one crowded out the other. Would it be conclusive to speak of higher competitive value and selection? It would certainly not be conclusive, except for the experimental conditions, the soil used, etc., and not for the varied conditions nature offers to the two, where such situations as in the experiment will hardly ever occur, and then only extremely locally, if ever. The very existence of the two species disproves already the assumption: in nature both occupy obviously their own particular ecology, otherwise one of the two would not exist.

Excretion in plants is mostly a physiological necessity. Dripping from hydathodes occurs when evaporation is insufficient: organic and mineral substances excreted in this way may serve animals. A similar reasoning could be held for excretions by glands.

Shelter is 'offered' by plants to animals, in many ways.

On the under-surface of leaves a fairly large number of woody plants develop domatia in the axils of the main nerves. The physiological function of these domatia is not known, according to Jacobs (1966), who published a classic paper on them. They do not excrete and are not glands; they appear often only when seedlings have reached a certain age. Their distribution in the plant kingdom is large but restricted; they have never been found in plants of arid countries. They were not infrequently termed '*acarodomatia*', derived from the observation that small arthropods seek shelter in these small cavities. It is proved that they originate irrespective of animal irritation and appear to be a whim of plant structure. The fact that animals exploit them as shelter means nothing special: animals will of course exploit anything they find favourable for their comfort and survival, animate or inanimate, just as primitive man would employ anything which he found useful or of advantage. Our urgent strife of locating useful things is of course not different from the same urge in animals. In fact we and the animals are completely possessed by this strife. But from a strictly detached point of view there is every reason to accept that domatia are an irrelevant structure in plants which is secondarily exploited by animals. That is, if we really want to detach ourselves from the inherent prejudice that all characters of animate nature must have some useful meaning.

I am of course by no means the first who ventilates criticism and in this context I want to refer to Bateson (1894: 12) who "undertook the study of adaptation as a test to the theory of natural selection and the hypothesis that there is a tendency for useful structures to be retained and for useless parts to be lost. We have no right to consider the utility of a structure demonstrated, in the sense that we may use this demonstration as evidence of the causes which have led to its existence. In absence of correct and final estimates of utility, we must never use the utility as a point of departure in considering the manner of its origin. It thus happens that we can only get an indefinite knowledge of adaptation, which is not an advance beyond the original knowledge that organisms are more or less adapted to their circumstances. No amount of evidence of the same kind will carry us beyond this point".

If we cannot perform this mental effort towards objectivity we will have to account for the presence of hairs, stipules, phyllotaxis, etc. etc. as well as for their absence in terms of utility. "No doubt", Bateson (1894: 79) says, "that ingenious persons would find ecological explanations of all these characters, for on this class of speculation the only limitations are those of the ingenuity of the author".

Various kinds of shelter are employed by ants in tropical plants. In these myrmecophilous plants the devices may be very simple, stem-appressed leaves of root-climbing plants (*Hoya, Dischidia*), reflexed appressed lowest pinnae of palm fronds (*Calamus* sp.), palm-sheaths (*Korthalsia*), appressed stipules, saccate domatia (several neotropical Melastomataceae, *Callicarpa saccata* van Steenis), but also pithy stems (*Cecropia, Endospermum* spp., *Clerodendrum fistulosum* Becc.) and pithy branches in a large number of Malesian trees of various families, the tendril of one species of *Nepenthes*, and stipular thorns of*Acacia*, in which the pith is removed to shelter ant colonies. The most spectacular shelter is offered by the root tubers of the epiphytic rubiaceous genera *Myrmecodia, Hydnophytum* and some allied genera. These tubers have large labyrinth-like cavities inhabited by ant colonies where they tend fungal gardens as food.

There is a host of literature on this subject, a survey of which would fill a book in itself. The essential question turns round the adaptation theory of Beccari (1884-1886) and Schimper (1888) who advanced that such structures in plants arose by the mutual action of plants and animals to the advantage of both. And they tried to collect data to show the advantage of ants for plants. The latter evidence appears, however, very dubious indeed.

One crucial point has been cleared by Treub (1883) who showed that the cavities in the *Myrmecodia* tubers originate already in seedlings without any action of ants and excellent upgrowth follows without them. Whether these cavities have any ecological meaning to the plant is uncertain; they may physiologically serve for aeration or evaporation for regulation of temperature, but this has not been proved.

It is doubtful even, whether they are essential to the ants. We note in this context, that certain European ants build their nests around the base of plants, preferably Rosaceae and Umbelliferae, but they survive equally well without them.

It stands to reason, however, that in an objective view there is no necessity to assume co-evolution, if we advance that these structures would also have been developed by plants without any ants in existence. Why should not leaves be appressed to stems in root-climbers, stipules leave cavities, leaves have domatia, pinnae be reflexed, stems and thorns have pith, all representing structural developments *sui generis*?

Conversely, it is clear that if ants evolved and would find these structures, they would employ them and take full advantage. Some species might even become entirely dependent.

Plant structure evolves first and it is the animals which will adapt themselves and often will evolve to greater specialization. This principle applies to chemical differentiation as well.

It has sometimes been advanced that the supposed profit the plants would have from the ants would consist of protection against other predators, but this is proved to be a fallacy. For *Myrmecodia* the profit for the plant was supposed to consist in accumulating minerals etc. for growth, but there are many large woody epiphytes without ants showing that in this aspect epiphytes can well manage this themselves. Then it was advanced that for several other myrmecophytes the ants are attracted by their seeds with their oil-containing elaiosome, which seeds are deposited in their nests. This is true and may locally add to their frequency, but none of these ant plants is confined to ant nests and their seeds can germinate on any suitable bark.

It must be concluded that the co-evolution of ants and plants is only a one-sided evolution, namely for the ants.

I fully agree with von Ihering (1907: 710) who said that *Cecropia* needs its ants as much as a dog its fleas.

Evolution of orchids

The spectacular development of Orchidaceae is of course a classic of co-evolution. Leaving apart a fairly considerable number of orchids which are self-fertilizers or are cleistogamous, the majority is compulsory cross-fertilized by insects and this has led to most ingenious devices of the orchid labellum.

Systematically the queer fact is that in orchids so many generic hybrids are found, and that still more can be made by artificial insemination. The definite impression is that the whole of the family is genetically only one comparium with many commiscua, and that the species are usually convivia. They maintain their distinction by the grace of compulsory cross-pollination and the use of selected insect species to achieve that goal. Orchid evolution thus reflects insect evolution.

As soon as in the variability range of an orchid a deviation, differing only in a few genes presumably, occurs, it may be favoured with an insect form from the variability range of the latter's population and the two will consequently form a couple of consorts. This is the first step towards more specialized couples of orchid/insect.

Here again, however, the deviating plant structure comes first; if there is no suitable insect partner, it will probably succumb; if there is a more or less suitable partner attracted by colour, shape, scent, etc., within the range of variability of the insect population, the couple is formed and the new plant is saved and lives on by the grace of the pollinating insect. The latter is of course in no way dependent on the orchid for its survival.

It cannot be the reverse, as there can be no stimulant or inductive influence emanating from an insect causing a plant towards a gene combination which it wants to have. Plant structure comes first, animal adaptation may follow.

Though we conclude that thus evolution in orchids will have been effected in a gliding way, imitating that of animals, saltations may occur by hybridization. It is namely known that insects may, incidentally, make errors in pollination by which even intergeneric fertile hybrids may occur. Their offspring will in subsequent generations produce a host of new forms which may again start couples with other insects and consequently lead to further form-development.

This sudden occurrence of hybrids may be termed 'saltatory', but for the essential difference that the saltation is of a much lower status than that discussed for other plants, as all the offspring remains within the orchid comparium in a net of interfertility.

A further curious observation can be made in orchids, *viz.* that by a single other 'saltation' the orchid flower does not develop in the proverbial bisymmetrical way, but as a normal regular monocotyledonous flower. Such 'peloric' forms, of which I have formerly listed some from the tropics (1949: xli-xlii), are only recognizable vegetatively by comparison, otherwise they are unidentifiable, even by first-grade specialists.

Whereas pelorias are generally caused only by one or a very few gene changes, this tallies with the considerations above that obviously the most remarkable build-up of the orchid labellum may be a beautiful façade, but that it is genetically and hence, taxonomically, not such a stable component.

It shows also that few genes may, in cases, bring about a sudden radical change in morphogenesis.

Evolution of figs

The evolution of figs is a culmination point of co-evolution, as here the pollinating wasps have still more specialized relations with the plant in that also their life is bound to the figs in a most intimate way, a compulsory symbiosis. This is certainly not so with orchid insects, not even in the highly specialized cases of pseudo-copulation. Much of what I have said about the relations between orchids and insects will hold here too.

New forms of *Ficus* will arise and succeed if from the variability of the insect populations a more or less suitable mate is available. If it is available, adaptation of a new insect population will follow. Much of this evolution seems not to have been competitive. Evolution seems to have resulted from the "extremely gradual alteration of the *Ficus*-protoplasm" (Corner, 1961: 113). In this aspect it is noteworthy that all species of *Ficus* seem to have the same chromosome number, $x = 13$.

If this assumption is true it would theoretically follow that artificial insemination of closely allied species of figs would in all probability lead to fertile hybrids. I am not aware that such crucial, certainly difficult experiments have ever been carried out.

A conclusion on this chapter on co-evolution runs as follows:

(i) In a large number of situations attributed to co-evolution, evolution is primarily of the animals. Plant structures are utilized by animals for their benefit and they specialize. The plant structures arose *sui generis* and not in so-called 'response' to animal agency.

(ii) Even in the vital association of insects and flowers in orchids and insects and figs in *Ficus* plants change (evolve) independently in an autonomous way and insects adapt themselves.

(iii) Speciation in orchids and figs imitates (follows) the gliding evolution as is usual in animals. Small changes accumulate in populations which diverge and gradually develop into races, subspecies and species respectively which in nature gain (ecological) isolation through the coupling with the particular insects. Insects are thus secondarily stimulated towards further evolution themselves.

(iv) Saltatory evolution in both groups, more especially in orchids, may occur incidentally through hybridization.

8. **Reticulate phylogeny**

I have termed this chapter reticulate phylogeny instead of reticulate affinity, because it concerns real ancestry which is meant here.

In general plant evolution through speciation will run divergent as in the branching mode of a tree, similarly as in animal evolution. Fig. 2.

There are, however, many instances known of allopolyploid species hybrids which are truly new species; they certainly in part share the characters of the two parent species but exhibit also new characters of their own.

By definition genetical contacts are prohibited between comparia. In plants a *comparium* is not rarely equivalent with a subgenus or genus, and as a rule species of different genera are incompatible and merging or exchange of genetical material is excluded.

However, exceptions occur, and there are several cases known where clearly through previous hybridization different generic genomes were blended through allopolyploidy. In the Cruciferae an allopolyploid generic hybrid was made between *Brassica* and *Raphanus*. Many genera are supposed to have originated in this way, e.g. *Armoracia*, and certain allopolyploid species known in Gramineae from parents belonging to different genera, such as *Aegilops* and *Triticum*, *Agropyron* and *Elymus*, etc. As early as 1881 Focke mentioned generic hybrids from the families Amaryllidaceae, Cactaceae, Campanulaceae, Compositae, Ericaceae, Gesneriaceae, Rubiaceae, and Scrophulariaceae; others have been found since. This opens the possibility for allopolyploidy.

I would certainly not suggest that all cases of reticulate affinity, a phenomenon which occurs frequently in plants, should be deemed to be the result of reticulate phylogeny.

On the other hand I suppose that in very many cases allopolyploid genera and species have as yet not been recognized as such and my estimate is that there is a fair number of them.

Allopolyploid blending means that two divergent 'twigs' of the ancestral trees are joined which caused a local 'netting' of its 'canopy'. There is good reason to suppose that this 'intertwining' has also acted in the past during the ancestral development of the plant kingdom. See fig. 2.

I emphasize that these allopolyploids may be extremely important in plant evolution, as from them other types, aneuploid, dysploid, or polyploid, may have originated.

Compared with plants such reticulate phylogeny may be tacitly assumed to be in the great minority in animal evolution. This is quite obvious, because sexual selection will prohibit to no mean degree genetical contacts at the level of species and genus. It makes it especially unlikely, or very rare, because in animals sexual behaviour, attraction and structure of the sexual organs play such an important rôle in the divergence of populations. Many 'experimental' specific and few generic hybrids are known, especially among insects, birds and mammals. But they are sterile as a rule, and even hybrids on a racial or sub-species level in the animal kingdom are very often sterile, a situation which is exceptional among plants.

9. Embryology and ontogeny

The fact that embryological and subsequent ontogenetic development in animals is so different from that in plants must have had evolutionary implications.

In animals the development of the embryo leads via metamorphoses, eventually alternated by larval generations, to the mature stage, but from the start it concerns the whole individual and its complete organization. This changes and grows and differentiates by a long series of internal structural transformations; it is a closed system. It is thus quite conceivable that for animals the subsequent stages in ontogeny can to a certain degree reflect the sequence of phylogenetic stages, as defined in Haeckel's principle or law of biogenetics. It can also be assumed that genetical changes may occur at all stages of this 'centripetal' development.

This is essentially different in plants where development is centrifugal and structure is proportionally so simple. Though the individual in *statu nascendi* is as the embryo contained in the seed coat, the internal development concerns only the development of the archegonium to a mature seed. There is no question of further internal transformation; it is an open system. Reserve food is stored either in albumen or cotyledons or both, but there is no reason to assume that either of the two is a reflection of ancestry in shape or otherwise. It should be admitted that a few ancestral characters e.g. primary vascularization, may be preserved as vestiges, as in plants all parts are end-products preserved thanks to the presence of cell-walls.

Also the first leaves above the cotyledons cannot be seen as reflecting ancestral shape. The ancestral, primitive shape of the leaf in Angiosperms is, as Corner (1954) has argued, in all probability the compound leaf, as still retained in many tree families as a primitive character, token of possible derivation from compound-leaved seed ferns. It is not impossible that also the seed ferns had seedlings with simple leaves and that the whole complex of vegetative upgrowth of seed fern ancestors is *grosso modo* retained in certain woody families of Angiosperms.

Under this point of view the simple leaf is among Angiosperms a derived stage. Such reduction should be considered as a manifestation of neoteny (see p. 116) by which principle is meant that the new form is simplified as compared with its ancestor at attaining the fertile stage. Neoteny causes ontogeny to be condensed; it is probably as frequent in plants as it is in animals.

The matter considered in this essay has lingered in my thoughts for many decades, in fact since I was a student and studied Carl von Naegeli's 'Mechanisch-physiologische Theorie der Abstammungslehre'. I realize very well that it will be provocative to those thinking in neo-Darwinistic terms.

For these reason I felt it not unnecessary to feed some ideas to the biological world in honour of Professor Corner as a token of my admiration for his immense achievement in botany from his studies in the tropics and his admirable attempts to pour new wine in old vessels of biological theory.

I feel much indebted to my friend and colleague, Prof. Dr. H. Gloor, Geneva, for improvement of the text.

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